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Energy Expenditure of Free-Ranging Chicks of the Cape Gannet *Morus capensis*

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ABSTRACT

The Cape gannet *Morus capensis*, a large fish-eating seabird, is endemic to southern Africa. To study the energetics of nestling growth, we used the doubly labeled water technique to measure field metabolic rate (FMR) of nestlings, from hatchlings to large partly feathered chicks ($n = 17$) at Malgas Island, Saldanha Bay, South Africa. At the same time, the growth rate of a large sample of chicks was measured ($n = 338$). These data, together with literature values on resting metabolic rate and body composition, were used to construct and partition the nestling energy budget. Nestling FMR (kJ d^{-1}) increased with body mass according to $\text{FMR} = 1.23m^{0.923}$, $r^2 = 0.944$. Mass-specific FMR ($\text{FMR}_{\text{ratio}}$; $\text{kJ d}^{-1} \text{g}^{-3/4}$) was independent of chick age ($r^2 = 0.20$, $P > 0.05$); mean mass-specific FMR was 4.11 ± 1.28 , $n = 17$. Peak daily-metabolized energy (DME), which represents the maximum rate at which parents must supply their nestlings, occurred at age 71 d and was $2,141 \text{ kJ d}^{-1}$. Between the ages 51 and 92 d (43% of the fledging period), the DME of Cape gannet chicks was equal to or surpassed 90% of adult FMR at the nest. Energy demand during this period of peak DME represented 58% of the total metabolized energy, which was estimated at 150.1 MJ for an average chick during a 97-d period, from hatching to fledging. Sensitivity analysis of the energy budget indicated that the model was robust; the biggest source of error ($\pm 15\%$) was for the mass-FMR equation used in the model.

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Keywords: Cape gannet, *Morus capensis*, field metabolic rate, energy budget, chick growth, seabird.

Introduction

Energy requirement is such a fundamental process of life that an understanding of energy demands can provide important insights into the biology of organisms (i.e., adaptive strategies) for a range of theoretical questions (e.g., life-history theory) and applied problems (e.g., to determine the impact on fish stocks in the case of a marine species). In this way, energy is seen as a unit of common currency in a community of organisms and their environment (Wiens and Farmer 1996).

Most seabirds are central-place foragers, at least during the breeding season, because parents need to return regularly to their nest sites to incubate eggs and to brood and feed chicks. Additionally, pelagic seabirds have to travel long distances to their feeding grounds and find sufficient food distributed patchily over huge expanses of oceanic waters (Ashmole 1971; Furness and Monaghan 1987). Because of these constraints, seabirds have less energy available for reproduction per unit of energy consumed than terrestrial birds (Visser 2001).

During the breeding season, parents have to obtain sufficient food to cover both their own needs and those of their chick(s). Typically, food requirements of the entire family peak during the second half of the nestling period, when chicks are large and growth rate is high. If parents fail to meet the food requirements of their families at this stage, chicks' growth, rate of maturation, and, eventually, fitness are impacted. Even adult survival is threatened when food availability falls below a threshold. Breeding attempts are then abandoned, leaving the young to starve to death as the adults go in search of food elsewhere (Schreiber and Schreiber 1984). In colonial nesting species, adult mortality and total nest failure due to food shortage can take dramatic proportions; seabirds off Peru die by the million during strong El Niño–Southern Oscillation events (Jordan and Fuentes 1966; Duffy 1983).

Cape gannets *Morus capensis* are central-place foragers, having to fly long distances from their breeding colonies to obtain food and bring it back to their brood. Radiotelemetry data indicated that Cape gannets breeding at Malgas Island fly between 180 and 220 km per foraging trip (Adams and Navarro 2005). GPS tracking revealed large variation in foraging trip lengths, likely due to fluctuations in the fish prey distribution, with mean foraging trip length of $460 \pm 241 \text{ km}$ (Mullers and Navarro 2010). At-sea energy expenditure of Cape

gannets has been estimated between 5.5 and 6.5 times basal metabolic rate (BMR; Mullers et al. 2009b and Adams et al. 1991, respectively). In the context of the breeding season, parental foraging efficiency is expressed as the total food intake of the family divided by total parental energy spent. In general, parental foraging efficiencies of seabirds are much smaller than in terrestrial birds. This is probably the result of relatively low food densities in pelagic ecosystems. Therefore, to collect sufficient food, birds have to fly vast distances, which is energetically expensive. Moreover, Cape gannets have a higher absolute at-sea metabolic rate than other seabirds, 143% more than those using gliding flight and 34% more than those using nongliding flight (Adams et al. 1991). Given these considerations, it is not surprising that many seabird species, including the Cape gannet, manage to rear only one chick per season (Jarvis 1974). However, in good years Cape gannets are able to increase their foraging efforts and manage to fledge artificial twins quite successfully (Navarro 1991).

In this study, the doubly labeled water (DLW) technique was used to measure the field metabolic rate (FMR) of free-living Cape gannet chicks. The DLW measurements were combined with data on growth (Mullers et al. 2009a) and data on body composition (Navarro 1992) of Cape gannet nestlings to produce energy budgets of growing birds and to examine the energetic cost of breeding birds. Given the constraints imposed on growth by the unpredictability of food supply in seabirds, one could expect seabird chicks to have evolved adaptations to reduce their energy expenditure and/or their total metabolizable energy (TME; Weathers 1992). In this study we will test these hypotheses by comparing the mass-specific FMR of Cape gannet chicks to values reported in Weathers's (1992) review of nestling energy requirements and by comparing the TME of Cape gannet nestlings with that predicted from models presented by Weathers (1992) and Visser (2001). We also compare the energy budget of free-living Cape gannet chicks with that obtained from chicks reared in captivity by Cooper (1978) and with the energy budget of the congeneric northern gannet (Montevicchi et al. 1984).

Methods

Study Area

The study was conducted at Malgas Island (33°03'S, 17°55'E), Saldanha Bay, South Africa, over two breeding seasons, 2003–2004 and 2004–2005. This island lies along the Benguela Upwelling System in the west coast of South Africa (Duffy and La Cock 1985). The breeding population of Cape gannets at Malgas Island increased from 25,040 breeding pairs in 1956–1957 to a maximum of 56,376 breeding pairs in 1996–1997 and then decreased to 36,156 breeding pairs in 2005–2006 (Crawford et al. 2007).

Chick Growth

At the beginning of each field season, a sample of ca. 50 chicks in a range of sizes was marked with a numbered plastic ring

that was removed before fledging. Measurements were taken throughout their development, usually at 5–8-d intervals. To offset mortality and fledging, we added new chicks to the original sample during the course of the field season to maintain the number of chicks being monitored at any one time at ca. 50. On each bird, the following was measured: (1) culmen length, to the nearest 0.1 mm, using a dial calliper; (2) the length of the flattened wing cord, to the nearest millimeter, using a metal ruler; and (3) body mass, using the appropriate Salter spring balance: 200-g, 1-kg, and 5-kg capacity, with 2-, 5-, and 25-g accuracy, respectively. An overall mean growth curve was obtained by fitting a Gompertz model to the series obtained from 3-d moving-median mass for each day, from age 2 to 96 d inclusive. Similarly, growth curves were obtained for 19 percentiles, 5%–95% at 5% intervals, and a Gompertz model was fitted to each of these, providing a set of smooth growth paths. Such growth trajectories were subsequently used in the sensitivity analysis of the energy budget (see supplementary material, available online).

Chick Age Determination

For all chicks of unknown age, age was estimated from measurements of culmen or wing chord length, which were used in backtransformation growth models from a sample of known-age birds. These two structures grow at different rates; culmen grows rapidly during the first 3 wk, whereas wing chord initially grows slowly and from the second week grows almost linearly. Wing chord continues to grow after fledging, by which time it has reached 90% of the adult size. Chick's age d (in d) was predicted with one of the following models:

$$d = -\frac{\log_e(89.78 - c)/(6.15c)}{0.086}, \quad (1)$$

$$d = \frac{1.395 - \log_e(\log_e(588.8/w))}{0.0264}, \quad (2)$$

where c is the culmen length (mm) and w is the wing chord length (mm). Equation (1) was used for chicks where $w < 40$ mm; otherwise, equation (2) was used (Mullers et al. 2009a).

Energy Expenditure

We determined nestling FMR using the DLW technique (Lifson et al. 1955; LeFebvre 1964; Tatner and Bryant 1989; Speakman 1997), in which an estimate of CO₂ production is obtained from the loss rate of the stable isotopes ²H and ¹⁸O. The size of the initial body water pool was determined from initial dilution of ¹⁸O using the plateau method of calculation, and final body water pool was determined by percentage mass from the initial determination (Speakman 1997). The loss rate of ²H provides a measure of the water flux.

To determine the dosage of DLW, we conducted a pilot experiment in September 2002 to measure the rate of water

flux using ^2H -enriched water, employing a protocol similar to that employed for DLW. Chicks were injected with a dose of ^2H -enriched water (99.9 atom% ^2H). Chicks weighing less than 1 kg were given 0.5 mL of enriched water; heavier chicks received 1 mL. The final sample was taken 24 h later. From these measurements, we determined that the minimal dosage was 0.6 mL kg^{-1} and that the DLW experiments should be conducted over a 48-h period.

Trying to get an even spread of ages and sizes, we assessed nestling FMR in a random sample of chicks; 10 experiments were conducted in 2002–2003 and 7 in 2003–2004. Chicks were captured, measured for culmen and wing chord, weighed, and injected with DLW under the abdominal skin. Nestlings were returned to the nest for 1–1.5 h to allow the injected DLW to equilibrate with the body water pool and recaptured to take an initial blood sample. It was assumed that equilibration in chicks was reached within this period (Speakman 1997). About 3 mL of blood was drawn from a brachial vein. About $5 \mu\text{L}$ of blood was transferred into each of six $25\text{-}\mu\text{L}$ glass capillary tubes. The tubes were immediately flame sealed and refrigerated until analysis. After a target interval of 2 d, nestlings were recaptured, measured, and weighed and a final blood sample was taken.

The natural background isotope levels were determined from blood samples of four untreated chicks each season. The values for these background levels were according to expectations for seabirds (i.e., the isotopic composition of their body water is close to that of ocean water). The DLW used was gravimetrically mixed from pure deuterated ($>99.9\%$) water and highly enriched (95%) ^{18}O water, such that the mixture contained 60.5 atom% ^{18}O and 36.5 atom% ^2H .

Isotopes were analyzed at the Centre for Isotope Research (University of Groningen) using methods described in detail elsewhere (Visser and Schekkerman 1999; Schubert et al. 2008). In short, the blood in the capillary tubes was distilled in a vacuum line and brought into a standard vial for automatic injection into the isotope ratio mass spectrometer system. Local water standards (gravimetrically prepared from pure ^2H and ^{18}O water) that cover the entire enrichment range of the blood samples were applied for calibration purposes. The actual ^{18}O and ^2H measurements were performed in automatic batches using a high-temperature pyrolysis unit (Hekatech) coupled to a GVI Isoprime isotope ratio mass spectrometer for the actual isotope analysis (Gehre et al. 2004). Analysis of a single sample took ca. 25 min. In the complete analysis scheme, several quality checks are incorporated, including duplicate sample analysis, the spread of initial values for similar situations, the spread of $^2\text{H}/^{18}\text{O}$ enrichment ratios for initials and finals, and both absolute and relative differences.

Rates of water efflux and CO_2 production of nestlings were calculated from isotope turnover (assuming a single-pool model) using equation (7.17) of Speakman (1997), as rewritten by Visser (2001, eq. [13.9]):

$$r\text{CO}_2 = \frac{N}{2.078 \times (k_0 - k_d) - (r_G \times 0.025 \times N \times k_d)},$$

where $r\text{CO}_2$ (mol d^{-1}) is the rate of carbon dioxide produced; N (mol) is the size of the body water pool; k_0 and k_d (units d^{-1}) are the fractional turnover rates of ^2H and ^{18}O , respectively; and r_G (dimensionless) corresponds to the fraction of the water efflux lost through evaporative pathways. This equation uses a fractional evaporative water loss value of 25%, which has been validated by Visser and Schekkerman (1999). We converted rates of CO_2 production (l d^{-1}) to energy expenditure (kJ d^{-1}) assuming a respiration quotient equal to 0.72, with the energy equivalent of $27.33 \text{ kJ (L CO}_2\text{)}^{-1}$, as recommended by Visser (2001) for a fish-eating bird.

Energy Density

The energy density (ED), the energy content per unit of fresh mass (kJ g^{-1}) of chicks, is required to calculate the energy budget of a growing chick (Visser 2001). Navarro (1992) studied the body composition and ED of Cape gannet chicks and gave a relationship between ED and chick age. However, in the energy budget calculations, the relationship between ED and chick mass is required. To obtain this, the relationship between ED and mass was recalculated using Navarro's original data. A simple linear regression model was fitted to ED values in relation to the ratio of chick mass to mean fledging mass.

Nestling Energy Budget

Nestling daily metabolizable energy (DME) was estimated as the sum of the energy retained as new tissue (RE) and FMR, using empirically established allometric relationships between ED and mass and between FMR and mass. The energy budget was partitioned in four components: minimal resting metabolic rate, biosynthesis, thermoregulation plus activity, and energy retained. FMR measures the first three; the fourth is calculated from growth and ED data. Energy of biosynthesis was estimated using the conventional approach of multiplying the RE by 0.33, which represents a synthesis efficiency of 75% (Ricklefs 1974). The relationship $\text{DME} = \text{FMR}$ was assumed during weight recession, which represents catabolism of body stores, largely, fat deposits (Navarro 1992). The Gompertz model (eq. [3]; see "Results") was used for mass versus age until peak mass was achieved, and simple linear interpolation was used to describe mass during the short weight recession period. Because it was not feasible to undertake respirometry under field conditions, we estimated minimal resting metabolic rate using the BMR equation for all birds (Tieleman and Williams 2000, eq. [4]). Because BMR is defined as the minimal euthermic thermoneutral resting metabolic rate of no-growing individuals, we will use the term "minimal resting metabolic rate" (mRMR; kJ d^{-1}) for growing chicks. mRMR was thus estimated as $10^{[0.416 + 0.677 \times \log_{10}(M)]}$, where M is fresh mass (g). The mRMR curve thus produced was adjusted so that its starting point corresponded to the BMR predicted for hatching birds given by Klaassen and Drent (1991): $\text{BMR}_h = F \times 10^{[1.697 + 0.855 \times \log_{10}(M)]}$, where $F = 0.0201$ is the factor to convert milliliters O_2 to kilojoules. A sensitivity analysis was conducted

to investigate how TME was affected by changes to the parameters of the underlying models (see supplementary material).

Statistical Analysis

Computations and graphics were done using R (ver. 3.02 for Windows; R Development Core Team 2013). Regression models, including ANCOVAs, were fitted with the linear models (lm) function, whereas fitting of the Gompertz growth model was done with the nonlinear least squares (nls) function. Bootstrapping was done with the package boot (Fox 2002); all bootstrap confidence intervals correspond to the adjusted bootstrap percentile for 1,999 sample replicates. To examine the allometric scaling of various physiological variables with body mass, we log transformed (base 10) the data to fit the equations in their linear form using standard least squared regression techniques. Unless otherwise indicated, means are given ± 1 standard deviation.

Results

Growth

Over the two field seasons 1,620 sets of measurements were taken on 338 chicks. Of these, 45 measurements corresponded to chicks whose age estimates were more than 97 d and were excluded from subsequent analysis. Box-and-whisker plots of the chick mass together with the modeled growth curve over the two periods combined are given in figure 1. The Gompertz (Kaufmann 1981) model for the median was

$$M_t = 3,141 \times \exp(-\exp(-0.0501 \times (t - 29.1))), \quad (3)$$

where M_t is the predicted mass (g) at age t (d). The standard errors for the parameters of the model were 20.4, 0.0009, and 0.22 for the asymptote, growth rate, and inflection point, respectively. This model accounted for 99% of the variance of median mass. From age 92 d onward, chicks started to lose body mass and enter into the weight recession portion of the fledging period. For purposes of the energy budget calculation, weight recession was interpolated linearly between peak mass and fledging mass, which for the 50% quantile was 3,050 g at 91 d and 2,938 g at 97 d, respectively. Chick growth below the 40% quantile did not exhibit weight recession. Growth rate ranged from 0.0458 kg d⁻¹ for the 5% quantile to a maximum of 0.0589 kg d⁻¹ for the 95% quantile, whereas the inflection time followed an inverse relation with quantile, ranging from 33.5 to 26.4 d for the 5% and 95% quantiles, respectively (see supplementary material, table 1). More detailed description and analysis of the growth of Cape gannet chicks during the period of study are given elsewhere (Mullers et al. 2009b).

ED

The relationship between ED (kJ g⁻¹) and body mass was best described by the following model (fig. 2):

$$ED = 5.322 + 4.373 \times \left(\frac{m}{A}\right)^2, \quad (4)$$

$r^2 = 0.886$, $n = 21$, where m is body mass (g) and A is mean fledging mass (g). A was recalculated from Navarro (1991) for

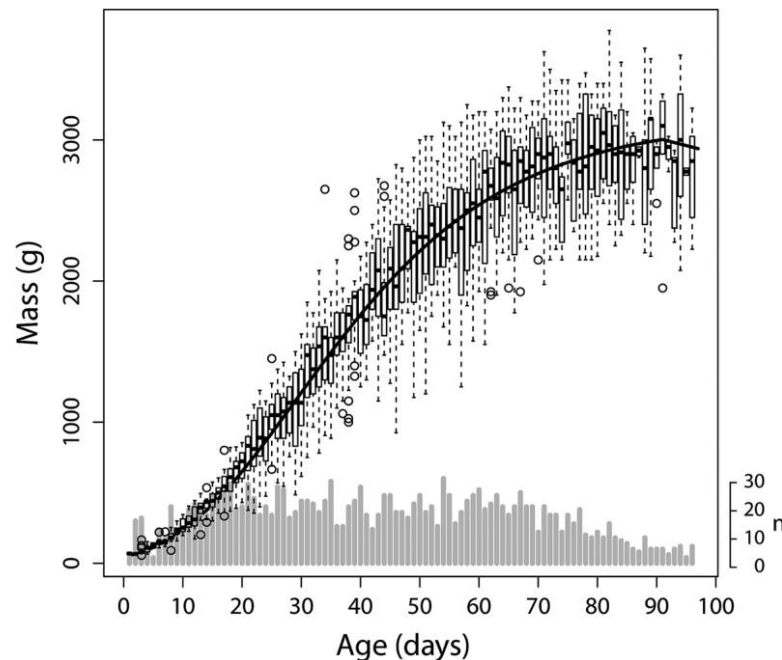


Figure 1. Box-and-whisker plot of body mass in relation to age of Cape gannet chicks at Malgas Island, over two breeding seasons, 2003–2004 and 2004–2005, based on 1,575 measurements on 338 chicks. Illustrated for each age are lower and upper quartiles (box) and the median (line across the box), the range of which is 0.75 times the box size over and below the median (whiskers); extreme values are shown separately (circles). A Gompertz model was fitted to the vector of medians (solid line). The bar graph at the bottom gives the sample sizes (n) for each age.

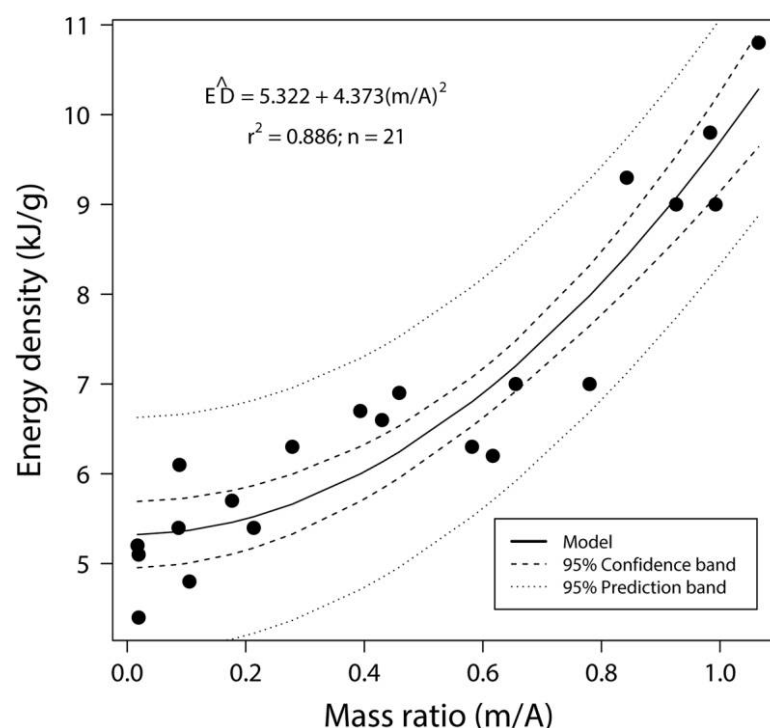


Figure 2. Energy density (ED; kJ g^{-1}) of Cape gannet chicks from Malgas Island, in relation to the mass ratio m/A , where m is body mass (g; wet) and A is asymptotic mass (g; wet); data from carcass analysis are by Navarro (1992).

34 control birds to be $3,051 \pm 257$ g (minimum = 2,300; lower quartile = 2,950; median = 3,075; upper quartile = 3,200; maximum = 3,400). This model provided a better fit than the three-parameter quadratic model (Akaike information criterion = 41.9 and 43.6, respectively), with the additional advantage of having one less parameter. Bootstrap confidence intervals were 5.006–5.613 and 3.637–4.960 for the intercept and slope, respectively.

FMR

The median elapsed time between initial and final blood samples was 48.0 h (range: 47.5–50.4 h), apart from one experiment that lasted 71.1 h, which was included in the analysis. The duration of the experiment was almost exactly a multiple of 24 h, as recommended for DLW experiments (Speakman 1997). There was no significant relationship between the CO_2 production and deviation of recapture from 24-h multiples ($r^2 = 0.09$, $P = 0.23$). Similarly, there was no relationship between the CO_2 production and the change in body mass ($r^2 = 0.08$, $P = 0.27$).

The FMR (kJ d^{-1}) determined from DLW experiments increased exponentially in relation to body mass (m ; g) according to the model

$$\text{FMR} = 1.23m^{0.923}, \quad (5)$$

$r^2 = 0.944$, $n = 17$ (fig. 3). Bootstrap confidence intervals for the power model were 0.70–3.04 and 0.78–1.01 for the intercept and exponent, respectively. The mass-specific FMR ($\text{FMR}_{\text{ratio}}$),

calculated by dividing the FMR value by mass to the $3/4$ power ratio (Weathers and Sullivan 1991), was independent of chick age ($r^2 = 0.05$, $P = 0.19$). Mean $\text{FMR}_{\text{ratio}}$ was 4.11 ± 1.28 ($\text{kJ d}^{-1} \text{g}^{-3/4}$), $n = 17$.

Energy Budget

The energy budget for a hypothetical chick growing along the median Gompertz trajectory is illustrated in figure 4. TME was estimated at 150,829 kJ for a 97-d fledging period. TME was partitioned as follows: mRMR 25.8%, RE (tissue deposition) 18.8%, cost of biosynthesis 6.2%, and activity plus thermoregulation 49.2%. Peak daily-metabolized energy occurred at age 71 d and was 2,141 kJ d^{-1} ; metabolized energy was more than 2,000 kJ d^{-1} between the ages 51 and 92 d, 43% of the fledging period.

Discussion

Growth Rate

Average growth of Cape gannet chicks reported in a previous study at Malgas Island (Navarro 1991) fell almost exactly along the 80% quantile trajectory of this study. Of the three parameters of the Gompertz model, only the asymptote of the previous study lay within the 95% confidence interval for the parameters. The growth rate in this study was below and the inflection time above the respective confidence intervals reported by Navarro (1991). Clearly, the growth performance

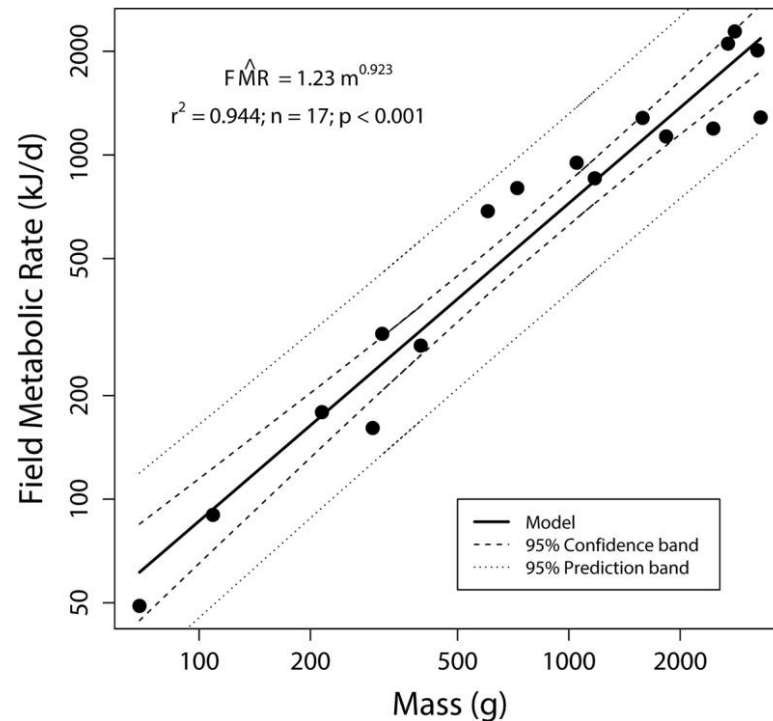


Figure 3. Relationship between field metabolic rate (FMR; kJ d^{-1}) and body mass (m ; g; average mass between initial and final samples) of Cape gannet chicks at Malgas Island, during the breeding seasons 2002–2003 and 2003–2004. FMR was measured using the doubly labeled water technique.

during the two seasons of this study was inferior to the growth performance during the 1986–1988 seasons. This decrease in growth performance seems most likely to be related to less favorable feeding conditions during this study, brought about by the eastward shift in the stocks of sardine (van der Lingen et al. 2005; Crawford et al. 2008), the preferred prey, becoming less accessible to gannets breeding at Malgas Island (Mullers et al. 2009a).

However, faster growth in Cape gannet chicks does not necessarily mean that fledging can be advanced because tissue and feathers need time to mature. For example, mean adult wing chord length is 478 mm ($\text{SD} = 12$; $n = 27$), whereas fledglings have a mean length of 431 mm ($\text{SD} = 27$; $n = 24$; R. Mullers, unpublished data), significantly shorter than the adult value ($t = 7.9$, $\text{df} = 30$, $P < 0.001$, Welch two-sample t -test). Furthermore, overweight fledglings are not capable of taking off and have to shed excess mass (fat deposits) before they depart from the island, and little parental care is provided to the chicks at this stage (Nelson 1978). Fledglings sometimes return to the nest site and persistently beg for another meal, but parents usually ignore them or move away from the nest site (R. A. Navarro, personal observation). The extra time required by chicks undergoing weight recession allowed additional time for growth of the primary wing feathers, a fitness factor that may be linked to the higher immediate postfledging survival of heavier fledglings reported by Jarvis (1974), alongside the more obvious benefit of having an energy re-

serve to see the birds through the initial mastering of their fishing skills (Navarro 1992). Weight recession is typical of seabirds with no parental care after fledging, a phenomenon similar to that shown by aerial foraging birds such as swallows (Hirundinidae; Lack 1968; Earlé and Underhill 1991).

FMR

The assumptions of the DLW method were reviewed by Speakman (1997). Of these, the one most likely to be violated is the assumption that the injected isotopes (^2H and ^{18}O) label the body water only. In growing birds, there is a high rate of synthesis of organic molecules, and it is likely that some of the ^2H and ^{18}O is removed from the body water pool and incorporated into tissue, which would cause an overestimate of the total body water (TBW) as well as the water flux rate (Williams and Nagy 1985). If ^{18}O is incorporated at a relatively lower rate than ^2H , the CO_2 production would be underestimated in proportion to the discrepancy in the incorporation rates of the two isotopes. This underestimation was suggested by Williams and Nagy (1985) to be as high as 25%. However, studies by Visser and Schekkerman (1999), Visser et al. (2000), and van Trigt et al. (2002) showed that the discrepancy was not caused by growth of the animal but rather by the assumption, built into the original equation of Lifson and McClintock (1966), that 50% of the body water leaves the animal through breathing, an isotopic fractionating pathway. Using a percent-

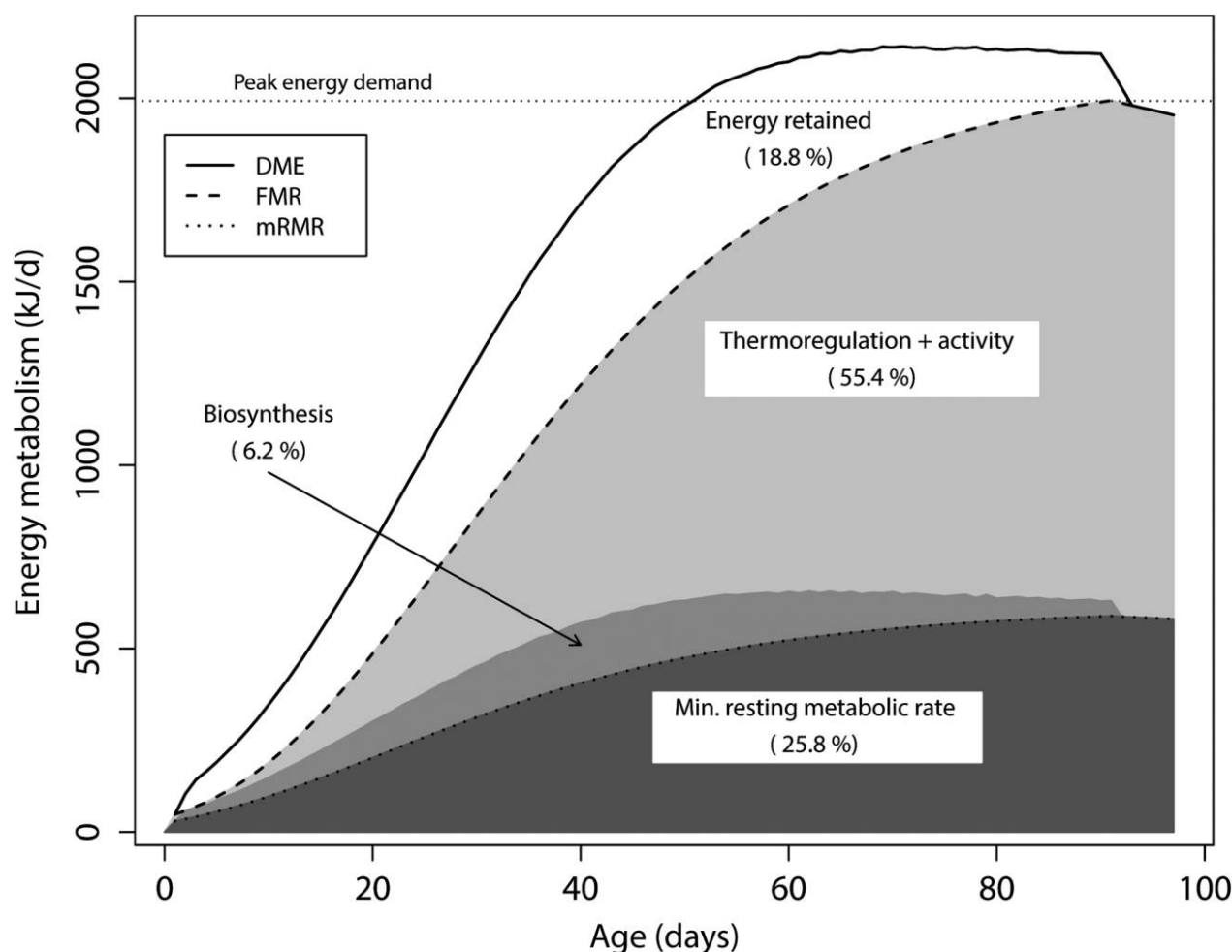


Figure 4. Energy budget of Cape gannet chicks at Malgas Island, over two breeding seasons, 2002–2003 and 2003–2004. The top line corresponds to the daily metabolizable energy (DME), the middle line represents the field metabolic rate (FMR) modeled from doubly labeled water measurements of free-ranging birds, and the bottom line represents the modeled minimum resting metabolic rate (mRMR) calculated from equation (4) for all birds in Tieleman and Williams (2000). The retained energy was calculated from energy density models based on carcass analysis (Navarro 1992). Peak demand (horizontal dotted line) was defined as 90% of the adult FMR at the nest ($2,214 \text{ kJ d}^{-1}$; Adams et al. 1991; the figure here has been reworked to account for the different value of energy equivalence used in their study).

age of 25%, as in the equation given by Speakman (1997, eq. [7.17]), leads to much better agreement, also in growing birds (average deviation was -2.9%). This equation has also been used in this study. Therefore, we are confident that the FMR values reported in this study are not underestimated by the high growth rate of Cape gannet chicks. Another check on the importance of tissue incorporation of the labeled isotopes is the comparison of TBW determination based on ^{18}O and ^2H (both from the initial injection). In all animals and under all circumstances, ^2H is indeed to some extent incorporated into tissue, which leads to a TBW estimate based on ^2H that is typically 1%–3% larger than that based on ^{18}O . In our study we found a difference of 1.7%, pointing in no way to an abnormal situation as far as tissue incorporation is concerned.

Comparisons across species must take into account the fact that FMR scales approximately to mass at the $3/4$ power (0.73 in Willmer et al. 2000). Thus, the mean mass-specific FMR ob-

served in this study (4.11 ± 1.28) was not significantly different from the mean across 30 species (4.01 ± 0.84 ; $t = 0.3$, $df = 23$, $P > 0.7$) quoted by Weathers (1992). The mass-specific FMR was calculated from data in Weathers (1992, table 1) by dividing TME by $\text{mass}^{3/4}$ and by days to fledging. This indicates general agreement with the pattern exhibited by species ranging in size from 9.7 g for white-bellied swiftlet *Collocalia esculenta* to 3,700 g for northern gannet and fledging periods from 8 to 97 d. Even when the sample is clearly biased toward the small species, with 25 of them weighing less than 500 g, Cape gannet chicks lie well within the observed pattern.

Energy Budget

At least one-third of the nestling period, between the ages 51 and 92 d (43% of the fledging period), the DME of Cape gannet chicks is equal to or surpasses 90% of adult FMR at the nest

(2,214 kJ d⁻¹; reworked from Adams et al. 1991, which used an energy equivalent of 25.8 kJ L⁻¹ CO₂). Energy demand during this period of peak DME represents 58% of TME.

According to Weathers (1992) the most important factors that determine TME required to produce a chick are body mass at fledging and the length of the nestling period. Weathers found that these two variables explained over 98% of the variance in TME in a sample of 30 species. This sample included the Cape gannet and northern gannet, both at the high end of the scale. The value predicted from Weathers's equation (8) for a Cape gannet chick ($TME = 6.65 \times m^{0.852} \times t_n^{0.710}$, where the fledging mass $m = 3,150$ g and the fledging period $t_n = 97$ d) is 163,678 kJ, 8.5% above the TME estimated in this study. Visser (2001) provides a similar equation for TME of seabirds, which gives a value of TME = 168,363 kJ, 11.6% over the value in this study. Weathers's predicted value corresponds to that of chicks at the 80% growth quantile, whereas Visser's value surpasses the TME of chicks in the 95% growth quantile. The lower than predicted TME of Cape gannet chicks probably points toward the presence of energy-saving mechanisms in this species, which would increase resilience to cope with unpredictable episodes of food shortage by lowering the energy demands of the chick.

Cooper (1978) measured metabolizable energy based on food consumption of two chicks reared in captivity, with TME being 185 MJ, 22% above the field value estimated in this study. It is important to note that Cooper's birds were fed to near satiation on a diet of anchovy *Engraulis encrasicolus*, one of the preferred preys of Cape gannets (Crawford and Dyer 1995). Montevicchi et al. (1984) estimated TME of northern gannet chicks at 145 MJ, 4% below the estimate for Cape gannet chicks; both species have similar fledging periods and masses. However, they estimated that about 44% of the chick's TME was allocated to growth (including the cost of biosynthesis) and as much as 33% was accumulated as tissue. This is in great contrast with the finding of this study that puts these figures at 25% and 18.8%, respectively. The difference in methodology, periodic weighing of four captive-reared chicks in the northern gannet study and DLW of 17 free-ranging chicks in this study, may account in large part for the great discrepancy in the energy allocation between the two species. Apart from the northern and Cape gannets, no other species of the family Sulidae has been studied with regard to chick energetics, so it is not possible to look for patterns. But it is expected that the closely related Australasian gannet *Morus serrator* shares a similar pattern of growth and energy allocation.

Conclusion

We tested two proposed mechanisms by which seabird chicks deal with the constraints on their growth. The mass-specific FMR of Cape gannet chicks was found to be within the range of other species' nestling energy requirements (Weathers 1992) and therefore does not seem to be a mechanism to adapt to the unpredictability in food supply. However, Cape gannet chicks do have a lower TME than could be expected for a species with

similar fledging mass and period (Weathers 1992). We therefore suggest that Cape gannets have reduced TME as an adaptation to periods of lower food availability.

The TME for growing Cape gannet chicks was 150,829 kJ. To sustain the growth of their offspring and fledge these successfully, gannet parents need to provide their chicks with 237 g d⁻¹ of sardines or 502 g d⁻¹ of hake (fisheries offal), based on an energy content of 8.59 and 4.07 kJ g⁻¹ of sardine and hake, respectively (Batchelor and Ross 1984), and an assimilation coefficient of 0.761 (Cooper 1978). During peak requirements, a chick would need 327 g d⁻¹ of sardines or 690 g d⁻¹ of hake. Each parent would thus have an additional energy requirement of 778 kJ d⁻¹ during chick rearing and 1,070 kJ d⁻¹ during peak growth, a substantial increase in their energy requirements. The lower TME would decrease the total energy expenditure of the energetically costly period during chick rearing of Cape gannet parents, a valuable adaptation in their life history.

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